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On the Identity of “*Zygodontomys*” *punctulatus* (Rodentia: Muroidea)

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ABSTRACT

The muroid rodent *Akodon punctulatus* Thomas was referred by Gyldenstolpe in 1932 to *Zygodontomys*, where it has remained to the present time. The species is known from the holotype collected in “Ecuador,” another specimen from “Bogota,” and a small series of skulls recently discov-

ered in the collections of the American Museum of Natural History, also from “Ecuador.” Reexamination of this material indicates that *punctulatus* is a species of *Bolomys* closely resembling *B. lasiurus*. The probable geographic origin of the few known specimens is discussed at length.

RESUMEN

El roedor muroide *Akodon punctulatus* Thomas fue referido por Gyldenstolpe en el año 1932 al género *Zygodontomys* donde se dejó hasta el presente. La especie se conoce del holotipo colectado en “Ecuador,” otro ejemplar de “Bogota,” y una serie de cráneos recientemente descubiertos en las

colecciones del Museo Americano de Historia Natural, también de “Ecuador.” El re-examen de este material indica que *punctulatus* es una especie de *Bolomys* asemejándose mucho a *B. lasiurus*. El probable origen geográfico de los pocos especímenes conocidos se discute a profundidad.

INTRODUCTION

In the course of revising the Neotropical muroid rodent genus *Zygodontomys* (Voss, in press), I examined the holotype of *Z. punctulatus* in the British Museum (Natural History). The specimen, collected by Louis Fraser in Ecuador sometime between 1857 and 1859, was a zoogeographic enigma. Although *Zygodontomys* is plentiful in some parts of Colombia, only this solitary example of the

genus had ever been reported from Ecuador. Since Cabrera (1961), Hershkovitz (1962), and Reig (1986) all regarded *punctulatus* as conspecific with various nominal forms of *Zygodontomys* (sensu stricto), I was surprised to discover that the holotype instead agrees in all qualitative characters of the skull and dentition with *Bolomys lasiurus*, an unrelated akodont widely distributed in the trans-

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Amazonian lowlands of Brazil, Paraguay, and eastern Bolivia. The purpose of this paper is to document the taxonomic history of the species originally described by Thomas (1894) as *Akodon punctulatus*, to describe the type and other available specimens, and to discuss the confusing geographic provenance of this material.

HISTORICAL BACKGROUND

Oldfield Thomas was not satisfied with his placement of *punctulatus* in the genus *Akodon* and remarked in the original description that,

This peculiar-looking species is of somewhat doubtful position, as its comparatively short crisp fur and, especially, its beaded supraorbital edges separate it widely from any other *Acodon* [sic]. In fact I think that it is nearly certain hereafter to require generic or subgeneric separation; but this can only be done when our knowledge of the whole group is much further advanced than at present. It is, however, possible that, in company with some other beaded species which have been referred to *Acodon* on account of their external proportions, such as *A. lasiurus* Lund, *A. punctulatus* should properly be placed in *Oryzomys*, of which it and they would then form a special group of short-tailed species. (Thomas, 1894: 362)

But *Oryzomys* already contained short-tailed species, namely *O. breviceauda* Allen (from Trinidad), and *O. microtinus* Thomas (from Surinam, and named in the same paper as *Akodon punctulatus*). In 1897, J. A. Allen erected *Zygodontomys* with type species *O. cherriei* (from Costa Rica) and also transferred *O. breviceauda* to the new genus. Thomas (1898: 270) named another species, *Z. brunneus* (from Colombia), and transferred his *O. microtinus* to *Zygodontomys*, observing that "... these short-tailed rats allied to *Oryzomys* seem to form a natural group, and there is a convenience in their having a special name." Why Thomas did not also transfer *Akodon punctulatus* and *A. lasiurus* to *Zygodontomys* in 1898 is not clear, but a few years later he concluded that "... Lund's *Mus lasiurus* ... is a *Zygodontomys*, and has nothing to do with the *Akodon* group" (Thomas, 1902: 61). Therefore, when Gyldenstolpe (1932) finally referred *punctulatus* to *Zygodontomys* (without comment), he was only

following a course of action implicit in Thomas's earlier remarks.

That the contents of *Zygodontomys* were heterogeneous was first realized by Tate (1939) who suggested that the nominal species occurring south of the Amazon (*fuscinus*, *lasiurus*, *lenguarum*, and *tapiripoanus*) were really *Akodon* after all. Ellerman (1941) and Cabrera (1961), however, continued to follow Gyldenstolpe by retaining *lasiurus* and its southern allies in *Zygodontomys*. In Hershkovitz's (1962) influential revision, only two species of *Zygodontomys* were recognized: *Z. breviceauda* (including *punctulatus* and other taxa from Central America and northern South America) and *Z. lasiurus* (which included all of the transAmazonian forms).

Subsequent cytological and morphological investigations have convincingly demonstrated that *lasiurus* (sensu Hershkovitz) is closely related to *Akodon* (Gardner and Patton, 1976; Reig, 1978; Maia and Langguth, 1981; Voss and Linzey, 1981) and the species is currently referred to the akodont genus *Bolomys* (e.g., by Reig, 1978, 1987; Macedo and Mares, 1987; and Anderson and Olds, 1989). Despite Thomas's early perception that *punctulatus* and *lasiurus* are similar, the former taxon has remained in *Zygodontomys*, perhaps because of its geographic proximity to members of the northern *breviceauda* group (of Hershkovitz, 1962). In fact, *punctulatus* is indistinguishable from *lasiurus* in qualitative external and craniodental characters and the two should be classified as congeners.

Below I redescribe the holotype and additional specimens of *punctulatus*, with special attention to the characters in which they differ from *Zygodontomys* and resemble *Bolomys lasiurus*. For the sake of descriptive economy it is assumed that the reader has ready access to my recent revision of *Zygodontomys* (Voss, in press) in which most of these characters are illustrated.

THE HOLOTYPE

The holotype of *Akodon punctulatus* (BMNH 59.11.1.8) is of unknown sex and consists of a skin accompanied by a skull and mandibles. The skin is intact but the skull is represented only by the facial skeleton (including the entire left upper molar row and

right M1-2) and the roof of the braincase. The entire basicranium, both auditory bullae, and the pterygoid region are missing. Despite this fragmentary material, enough remains to establish that *punctulatus* is unlike any member of the genus *Zygodontomys*.

1. Although grossly similar to *Zygodontomys* in external appearance, *punctulatus* differs in several points. While not strictly naked, the ears and tail of *Zygodontomys* are only sparsely provided with short hairs; the skin of the ears is quite visible and the epidermal scales of the tail are conspicuous. By contrast, the skin of the ears of *punctulatus* is entirely concealed by short, grizzled hairs, and the epidermal scales of the tail are almost invisible beneath a denser caudal pelage.

2. The hindfoot is narrower in proportion to its length in *punctulatus* than in any species of *Zygodontomys*, and digit V is much shorter in relation to IV. In *Zygodontomys*, the claw of V extends to the first interphalangeal joint of IV, but in *punctulatus* the claw of V extends only about one-half or two-thirds the length of the first phalange of IV.

3. The upper incisors of *punctulatus* are more procumbent, almost orthodont, by comparison with the strongly opisthodont orientation of these teeth in *Zygodontomys*, and other characters of the rostral region covary with incisor morphology. The nasal bones are shorter in *punctulatus* than in *Zygodontomys*, terminating anteriorly only slightly beyond the premaxillae; in consequence, the procumbent incisors are exposed to dorsal view in front of the nasal tips. In *Zygodontomys* the nasals project well beyond the premaxillae and the incisors are never visible in dorsal view. In lateral view, the rostrum of *punctulatus* tapers much more abruptly, from its deepest profile (above the maxillary zygomatic root) to its narrowest point (just behind the incisors); the rostrum of *Zygodontomys* is deeper throughout its length.

4. The slitlike incisive foramina of *punctulatus* are widest at the premaxillary/maxillary suture and taper only slightly posteriorly, appearing almost parallel-sided by contrast with the widely open, ovate foramina of *Zygodontomys* (which are widest behind the premaxillary/maxillary suture).

5. The molar dentition is much worn in

the type of *punctulatus*, but enough occlusal detail remains to determine that the principal labial and lingual cusps alternate in their anteroposterior position down the long axis of the tooththrow instead of being arrayed in opposite pairs as in *Zygodontomys*. Additionally, a small but distinct paralophule projects from the paracone of the first upper molars of the type of *punctulatus* (second molars are too worn to determine occlusal details). This accessory enameled structure is absent from the molar dentition of *Zygodontomys*.

6. The first upper molar of *punctulatus* has a fourth, labial root (above the paracone) in addition to the anterior, posterior, and lingual roots present in *Zygodontomys*. The first lower molar of *punctulatus* has a labial root (below the protoconid) and a lingual root (below the metaconid) in addition to the anterior and posterior roots present in *Zygodontomys*.

7. The capsular process of the lower incisor alveolus is situated well behind the coronoid process on the lateral surface of the mandible in *punctulatus* by contrast with the position of the capsular process almost directly beneath the coronoid in *Zygodontomys*.

OTHER SPECIMENS

Besides the holotype there is one more example in the British Museum collections identified by Oldfield Thomas as *punctulatus*. This specimen (BMNH 41.590) consists of a skin with a skull and mandibles. The skin has been chemically cured, and perforations in the wrists and heels suggest that it was once mounted in a lifelike pose and attached to a base by wires; large patches of fur are missing from the nape and shoulders, face, flanks, and belly. All of the ventral surface of the skull behind the molar rows is missing as are both zygomatic arches; the roof of the braincase is supported and attached to the facial skeleton by a mass of glue and cotton fiber. The angular processes of both mandibles are also missing.

The British Museum's Zoological Accessions Register (Vertebrates) for 1841 gives the identification of 41.590 as *Mus arviculoides* and the locality as the "Brazils." The specimen was one of a lot purchased from

TABLE 1

Craniodental Measurements^a (in millimeters) of *Bolomys punctulatus* (The mean, the range in parentheses, and the sample size are provided for Richardson's specimens.)

	British museum specimens		Richardson's Specimens ^c
	59.11.1.8 ^b	41.590	
CIL	—	—	27.0 (26.4–27.4) 4
LD	8.5	7.9	7.9 (7.6–8.5) 6
LM	4.3	4.8	4.7 (4.4–4.9) 8
BM1	1.4	1.4	1.4 (1.3–1.4) 8
LIF	—	6.6	6.2 (6.0–6.4) 7
BR	4.7	—	4.5 (4.2–5.0) 7
BPB	—	—	2.9 (2.6–3.1) 5
BZP	3.3	—	2.9 (2.8–3.0) 7
LIB	4.8	5.0	4.8 (4.5–5.0) 8
BB	12.2	—	12.4 (12.2–12.5) 5
DI	1.5	1.4	1.4 (1.2–1.4) 8
LOF	10.4	—	10.0 (9.4–10.3) 4

^a As defined and illustrated by Voss (in press).
^b The holotype.
^c AMNH 36312, 41015, 41023, 41024, 41025, 41026, 41028, 41029.

“Parreys” (probably a commercial taxidermist) that included other tropical South American species, but also specimens from Dalmatia, Java, Mexico, Siberia, and Switzerland. The tags attached to the skin and skull of 41.590 are in Thomas’s hand and give the locality as “Bogota” (on the skull tag) and “Sta. Fe de Bogota” (on the skin tag). On the reverse of the skin tag Thomas noted “Unstuffed 10/94. Locality painted on stand,” confirming the inference that the skin was originally mounted, probably with the skull inside.

Although there are sufficient points of resemblance between the type of *punctulatus* and BMNH 41.590 to lend credence to Thomas’s judgment that the two specimens are conspecific, the cranial skeleton of the latter is so badly damaged as to provide no further information worthy of record. Happily, additional material was recently discovered by Dr. Guy G. Musser among some unidentified specimens in the collections of the American Museum of Natural History.

The new material consists of eight skulls, unaccompanied by skins, collected by William B. Richardson in Ecuador. Measure-

ments of these specimens (table 1) compare plausibly with those of the type and BMNH 41.590, and the new skulls also agree with the type in all of the qualitative characters that can be determined from the latter. The cranial and dental morphology of *punctulatus* can now be redescribed and illustrated in enough detail to sustain confident taxonomic judgments.

BOLOMYS PUNCTULATUS (THOMAS, 1894)

- Acodon punctulatus* Thomas, 1894: 361.
- Akodon punctulatus* Trouessart, 1898: 536.
- Zygodontomys punctulatus* Gyldenstolpe, 1932: 114.
- Zygodontomys punctulatus punctulatus* Cabrera, 1961: 464.
- Zygodontomys brevicauda punctulatus* Hershkovitz, 1962: 204.

TYPE MATERIAL: As described above.

DISTRIBUTION: Somewhere in Ecuador and perhaps also in Colombia (see discussion of locality data below).

CRANIODENTAL CHARACTERS: In dorsal view, the skull of *punctulatus* (fig. 1) is characterized by short, truncated nasal bones; beaded, convergent supraorbital margins; convergent zygomatic arches, and a high, narrow braincase. Just behind the orbits, where the supraorbital bead contacts the temporal ridge on each side, a small, angular postorbital process is developed on most skulls. In lateral view, the rostrum tapers conspicuously as described earlier for the holotype, and this feature together with the truncated nasals and procumbent incisors lends the entire rostral region the same distinctive profile as that illustrated for *Bolomys lasiurus* by Voss (in press: figs. 5 and 9). The zygomatic plate is broad with a vertical anterior margin. The incisive foramina, usually widest at or near the premaxillary/maxillary suture, penetrate posteriorly between the anterocones or the protocones of the first molars. The bony palate is broad and short, not extending posteriorly beyond the third molars, and lacks conspicuous posterolateral pits. The mesopterygoid fossa is fenestrated by large sphenopalatine vacuities and the flanking parapterygoid fossae are narrow. A stout, vertical strut of the alisphenoid separates the buccinator-masticatory foramen from the ac-

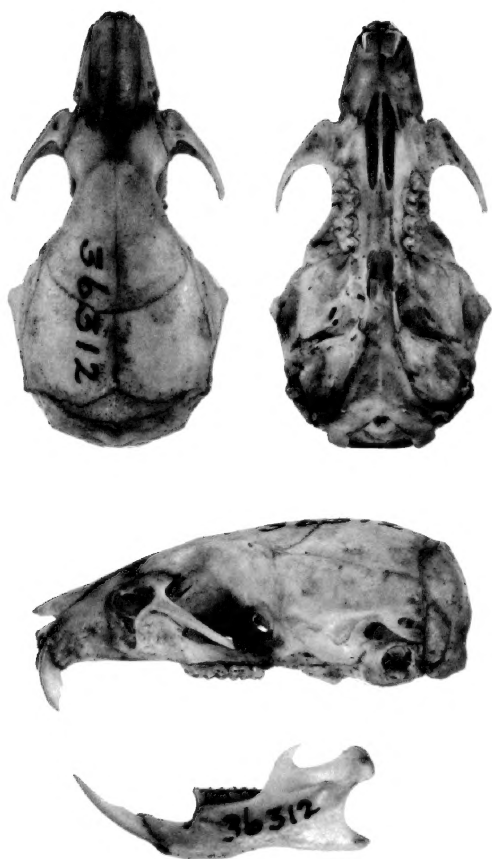


Fig. 1. Cranium and mandible of *Bolomys punctulatus* (AMNH 36312). About $\times 2$.

cessory oval foramen. The carotid circulation is primitive (resembling pattern 1 of Voss, 1988) with a supraorbital branch of the stapodial artery traversing the lateral wall of the braincase in a shallow internal groove that communicates with a small sphenofrontal foramen in the rear of the orbit. The auditory bullae are small and flask-shaped, and the lateral wall of the braincase above them on each side is perforated by the postglenoid foramen and a large subsquamosal fenestra. The capsular process of the lower incisor alveolus is situated well behind the base of the coronoid process on the lateral surface of the mandible.

The upper incisors are weakly opisthodont to orthodont, noticeably more procumbent than in most Neotropical muroid species. The principal labial and lingual cusps of upper and lower molars (fig. 2) alternate in antero-

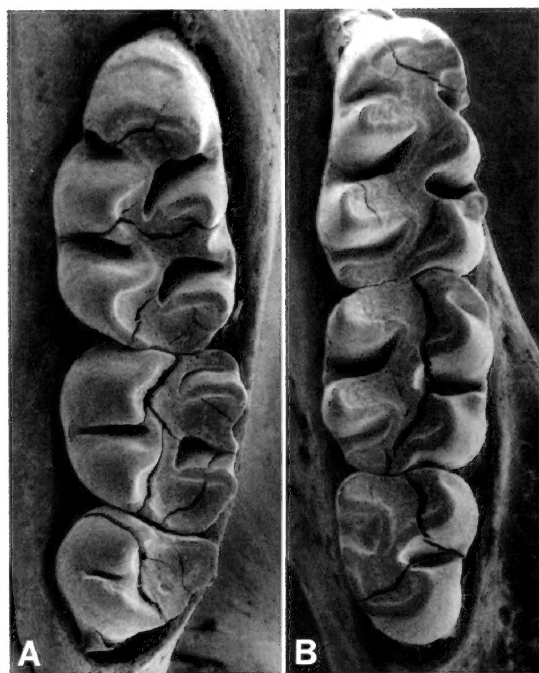


Fig. 2. Molar dentition of *Bolomys punctulatus*. A, left upper molars of AMNH 41026; B, right lower molars of AMNH 41015. About $\times 16$.

posterior position down the toothrow, and are not arranged in strictly opposite pairs. The anterocone of the first upper molar is entire and undivided, and small but distinct paralophules project posterolabially from the paracones of the first and second upper molars. The anteroconid of the first lower molar is also undivided, and the first and second lower molars are usually provided with small ectolophids (attached to the hypoconids) and entolophulids (attached to the entoconids). The first upper molar has four roots, and the first lower molar three or four (a small lingual root under the metaconid may be present or absent).

SPECIMENS EXAMINED: **Ecuador**—(no other locality data) AMNH 36312, 41015, 41023–41026, 41028, 41029; Pallatanga (?), BMNH 59.11.1.8 (the type). **Colombia** (?)—Bogotá (?), BMNH 41.590. Total, 10.

DISCUSSION

The muroid rodent described by Thomas (1894) as *Akodon punctulatus* differs from members of the genus *Zygodontomys* in the

morphology of the upper incisors and rostrum; the parallel shape of the incisive foramina; possession of a short bony palate; the absence of conspicuous posterolateral palatal pits; the presence of an alisphenoid strut separating the buccinator-masticatory and accessory oval foramina; the posterior position of the capsular process of the lower incisor alveolus; the alternate arrangement of molar cusps; the presence of accessory molar lophs(ids); and the number of roots of the first upper and lower molars. In each of these characters, *punctulatus* resembles *Bolomys lasiurus* (see Voss, in press), and these two taxa are actually so similar that I have been unable to find any point of consistent cranial or dental difference between them. Since *B. lasiurus* is an abundant species in trans-Amazonian Brazil, Paraguay, northern Argentina, and eastern Bolivia, whereas the few known specimens of *punctulatus* are supposedly from the northern Andean region, it is reasonable to question whether mistakes in the geographic data accompanying the latter are possible.

The type of *punctulatus* was stated by Thomas (1894) to have been collected by Louis Fraser in "Ecuador (probably Pallatanga)," but neither the British Museum's Accessions Register for 1859 nor the labels attached to BMNH 59.11.1.8 provide any locality information more specific than "Ecuador." Pallatanga (1°59'S, 78°57'W) is a town at 1500 m elevation on the Pacific slopes of the western Andean cordillera in Provincia Chimborazo (Paynter and Traylor, 1977) where Fraser worked from August through December 1858. Since Fraser traveled widely in Ecuador between September 1857 and December 1859, however, there appears to be no compelling reason (in the absence of Fraser's own collecting records) to assume that the type was actually collected at Pallatanga (see Gardner, 1983, for an account of Fraser's itinerary). On the other hand, there is no good reason to doubt that the specimen was obtained in Ecuador.

The provenance of the second BMNH example of *punctulatus*, BMNH 41.590, was documented only by the inscription "Bogota" or "Sta. Fe de Bogota" painted on the stand of the mounted skin as described earlier. Unfortunately, even this meager datum

is not to be trusted at face value since "Bogota" was indiscriminately employed by 19th century collectors for specimens taken in many different habitats on both sides of the eastern Andean cordillera of Colombia (see Chapman, 1917: 11–15).

W. B. Richardson's series of *punctulatus* in the American Museum of Natural History (AMNH 36312, 41015, 41023, 41024, 41025, 41026, 41028, and 41029) is a confusing lot. The skull-vial label of AMNH 36312 bears the information "Ecuador: Chimborazo, Jul. 3, 1913" on one side with the number 193 inked on the reverse. The catalog entry (dated 29 September 1913) for AMNH 36312, however, gives the identification as *Thomasomys paramorum*, and there is a skin and skull of *T. paramorum* from Chimborazo that bear this catalog number in the collections. Richardson's original label, a perforated piece of red cardboard attached with scarlet thread to the right hind foot of the *Thomasomys* skin, reads "193 Chimborazo 15000 [ft] July 3, 1913 WR" on one side and provides measurements on the other. The skull of the *Thomasomys* specimen, however, is not accompanied by one of the small metal tags that Richardson used to number his skulls, and no original number is recorded on the AMNH skull-vial label. The likeliest explanation for this duplication is that the *Thomasomys* skin and the *punctulatus* skull (both associated with Richardson's field number, 193) were mismatched (perhaps in the field) and that this error was subsequently corrected when an unassociated *Thomasomys* skull was discovered in the course of museum preparation; evidently, it was not deemed necessary to recatalog the *punctulatus* skull.

The other AMNH specimens of *punctulatus* are all accompanied by perforated metal tags bearing Richardson's field numbers (101, 240, 263, 264, 283, 285, and 291). These were cataloged sometime between 1919 and 1935 as *Mus musculus* with collection dates recorded as "June–July 1913"; the skull-vial labels of AMNH 41026 and 41029, however, give the year of collection as 1933 (presumably inadvertent transcription errors).

I have not been able to locate Richardson's original field catalogs and notes (if they ever existed) in the archives of either the Department of Ornithology or the Department of

Mammalogy at the American Museum of Natural History, but Richardson's itinerary in Ecuador can be reconstructed from his correspondence with Frank M. Chapman, then chairman of the Department of Ornithology. This mass of letters (in the Department of Ornithology archives) corroborates and amplifies the brief accounts of Richardson's travels published by Allen (1916) and Chapman (1926).

Richardson arrived in Ecuador at Esmeraldas in October 1912 and collected from then until the middle of May 1913 along the Pacific littoral, in the coastal hill country between Esmeraldas and Guayaquil, in the valley of the Río Daule, and on Isla Puná. June and July were mostly spent in the highlands (where Richardson visited Riobamba, Quito, Volcán Pichincha, Antisana, Corazón, and Chimborazo), but also in the western Andean foothills near Gualea; during these months Richardson purchased a quantity of mammal specimens from Ludovic Söderström, a diplomat and well-known professional collector resident at Quito. In August, Richardson returned to Guayaquil where he collected briefly before beginning preparations to visit the eastern lowlands. Leaving Guayaquil around the first of September, Richardson arrived at Santa Rosa on the fifth and spent the next month collecting in the western foothills of southern Ecuador, notably at Portovelo and Zaruma. Richardson left Zaruma in early October, crossed the Andes, and descended the eastern slopes to Zamora where he stayed for about a month. By late November Richardson was back at Santa Rosa and by early December he was prostrated with malaria in Guayaquil. Richardson left Ecuador in January 1914.

Specimens collected by Richardson in 1913 could, therefore, have come from almost anywhere in Ecuador. If the "June–July" dates attributed to the specimens of *punctulatus* in the AMNH catalog are to be believed, the scope of inquiry is not much more restricted since Richardson ranged widely about the country in those months and also bought specimens from Söderström. In Allen's (1916) report on Richardson's collections, there is no reference to unidentified material that might represent this species.

In summary, the locality data associated

with all known specimens of *punctulatus* are less than satisfactory, but there seems little a priori justification for rejecting such information as does exist. That information consists of at least two independent records from Ecuador and one rather more dubious record from eastern Andean Colombia. To account for the absence of additional material from these relatively accessible regions, it can only be speculated that the habitats in which *punctulatus* occurs have not often been sampled by collectors.

The morphological data reviewed earlier provide unequivocal evidence that *punctulatus* is a species closely resembling *Bolomys lasiurus*, a conclusion that is also supported by comparisons of the craniodental measurements in table 1 with those of *B. lenguarum* (= *B. lasiurus*) tabulated by Anderson and Olds (1989). Nevertheless, it is premature to judge these taxa conspecific with the sparse material presently at hand for *punctulatus*, and in view of the wide geographic separation of their known ranges. Since *punctulatus* is clearly not a species of *Zygodontomys*, however, there can be no objection to its transfer to *Bolomys* with the expectation that this action will focus the attention of future researchers when better material becomes available.

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